Assessment of runner bean (*Phaseolus coccineus* L.) germplasm for tolerance to low temperature during early seedling growth

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Summary

The runner bean requires moderately high temperatures for optimum germination and growth. Low temperature at sowing delays both germination and plant emergence, and can reduce establishment of beans planted early in the growing season. The objective of this work was to identify potential runner bean germplasm with tolerance to low temperature and to assess the role of this germplasm for production and breeding. Seeds of 33 runner bean accessions were germinated in a climate-controlled chamber at optimal (17 ºC-day/15 ºC-night) and at sub-optimal (14 ºC-day/8 ºC-night) temperature. The low temperature tolerance was evaluated on the basis of germination, earliness, ability to grow and vigor. Differences in agronomical characters were significant at low temperatures for germination, earliness, ability to grow and early vigor except for emergence score. The commercial cultivars Painted Lady Bi-color, Scarlet Emperor, the Rwanda cultivar NI-15c, and the Spanish cultivars PHA-0013, PHA-0133, PHA-0311, PHA-0664, and PHA-1025 exhibited the best performance under cold conditions.

Introduction

The scarlet runner or runner bean (*Phaseolus coccineus* L.) is a climbing perennial vegetable often grown as an annual crop for dry seeds or immature pod production, and also as an ornamental vine. This species is native to Mexico, Guatemala and Honduras, but the domestication area(s) is still unknown (Debouck and Smartt, 1995; Delgado, 1988; Freytag and Debouck, 2002). The runner bean was introduced into Europe from Central America. Seed exchange with Europe may have taken place when Europeans first visited the Americas, taking the attractively colored seeds back home to sow in their gardens (Zeven et al., 1993). Spain is purported to be the country of introduction into Europe, evidenced by the French name 'Haricot d'Espagne' that makes reference to the runner bean. The reason for its recent expansion as an ornamental plant in Europe may be the gaudy inflorescences.

Although of minor importance in the United States, the crop is of importance in some parts of South Africa and Europe (Mullins et al., 1999). The United Kingdom appears to be the major grower reflected by the large number of registered cultivars as either food sources or as ornamentals as compared with those of common bean (*Phaseolus vulgaris* L.) (Plant Varieties and Seeds Gazette, 2002). The reason scarlet runner beans are frequently grown in the United Kingdom is because they are better adapted to the cool temperatures than the common bean, and they produce a reliable crop of green beans for commercialization. In cold and wet summers, the common bean crop can often fail. In the Netherlands, people consume young pods or dry seeds of runner bean, but the crop is only grown in private gardens (Zeven et al., 1993). In South Italy and Spain consumers prefer the white seeded runner bean types (Campion and Servetti, 1991), commonly grown commercially on a small scale and many people

cultivate their own cultivars for niche markets. In the highlands of central Spain (Castilla y León) farmers often grow the extra-large white seeded cultivar 'Judión de la Granja', a cultivar with enough market value to compete with elite common bean cultivars. However, despite the potential of runner bean for breeding purposes, the germplasm of this species has not been adequately evaluated or used for the development of new breeding lines.

Researchers have successfully introgressed moderate levels of resistance to *Xanthomonas* (Miklas et al., 1994), *Fusarium* root rot (Wallace and Wilkinson, 1965), and white mold (Miklas et al., 1998, Lyons et al., 1987) from *P. coccineus* into *P. vulgaris*. Wilkinson (1983) suggested that the runner bean could be a potential source of high yield for common bean, but practical achievements in terms of the release of commercial cultivars have been few (Singh, 1992). A complete evaluation of runner bean cultivars could reveal the existence of potentially valuable traits, rare or non-existent in common bean germplasm, useful for improvement of the common bean. Santalla et al. (2004) reported the evaluation of runner bean cultivars from Spain for morphological, agronomical and seed quality traits in different environments. They found some valuable germplasm that could be of use either in production or breeding, including interspecific hybridization with common bean.

Most advances in early maturity of beans have been attained by selection for early flowering or early pod maturity. Little attention has been placed on selection for rapid germination and seedling development although it may affect early growth and flowering. As observed by the authors and local farmers the runner bean generally requires moderate temperatures for good germination and growth and the optimum temperature ranges from 20ºC to 30ºC (Association of Official Seed Analysts, 1981).

Other crops such as common (*P. vulgaris*) and tepary bean (*P. acutifolius*) do not emergence at 10ºC as reported by Scully and Waines (1987). Temperature is a limiting factor for bean production and low temperature at sowing delays both germination and plant emergence, lengthening the crop cycle and increasing production costs. An alternative to optimize the available growing period is to use cultivars that are more tolerant to low temperature at the germination and emergence stages (Otubo et al., 1996; Revilla et al., 2005). Little research has been done to obtain cultivars of this type. The identification of potential germplasm with tolerance to sub-optimum temperatures during early seedling growth may be of considerable value in the improvement of runner bean cultivars.

The objectives of this research were: i) to identify potential runner bean germplasm with tolerance to low or sub-optimal temperature during germination and early seedling growth and ii) to assess the potential of this germplasm for production and breeding.

Materials and Methods

Plant material. Thirty-three runner bean cultivars (Table 1) were evaluated in a climate-controlled chamber for tolerance to low temperature during early seedling growth. Seventeen of them were cultivars collected in different areas in the Iberian Peninsula, where traditional farming methods have encouraged the preservation of old cultivars. This genetic material is maintained in the germplasm collection at the MBG-CSIC (Misión Biológica de Galicia, Spanish Council for Scientific Research) and it was previously evaluated in field trials by Santalla et al. (2004). Two cultivars, PHA-0166 and PHA-1023, were heterogeneous for seed color and they were divided into sets of white and colored seed. Four cultivars and a wild population from Mexico and two cultivars from Rwanda were included in the experiment. They originate in cool highlands and could be a reference for this study. Two cultivars from Mexico, namely PI313313, PI325608 and the wild population PI53527 did not grow normally and they were not considered for further data collection and analysis. The two cultivars from Rwanda were also divided according to seed color. Five commercial runner bean cultivars from the United Kingdom were used as controls. The seeds used in the experiment were obtained from plants grown in the same environment in 2004.

Experimental design and growing conditions. Each accession was sown in sterile medium in plastic containers. Each container held 10 plants (one plot) with distance between plants of 2.5 cm and between rows of 5 cm. The experimental design was arranged as randomized complete blocks with three replications. The experiment included a sub-optimal temperature (t1) resembling the average weather in April (14 h days at 14 ºC and 60 % relative humidity and 10 h nights at 8 ºC and 80 % relative humidity) and an optimal growing temperature (t2) resembling the weather in May (15

h day at 17 ºC and 60% of relative humidity and 8 h night at 15 ºC and 80% relative humidity) in North-western Spain (42ºN, 8ºW). Irrigation was provided when needed. Light was provided by seven VHO (very high output) fluorescent lamps with a photosynthetic photon flux (PPF) of 228 μmol m^{-2} s^{-1}.

Data collection. Morphological and qualitative data were recorded at different plant stages (IBPGR, 1983). The seed weight (g 100 $seed^{-1}$) and the color and pattern of the seed coat of each accession were recorded before sowing. The following traits were determined for each plant under sub-optimal temperature: emergence (days from sowing to hypocotyl emergence), position of cotyledons after emergence (hypogeal, intermediate or epigeal), days to first trifoliate leaf (days from sowing to the first expanded trifoliate leaf), plant height (recorded in millimeters at 10 and 20 d after emergence), dry weight of root and aerial parts (measured in grams after drying at 80 ºC during 48 h when the first trifoliate leaf is opened and the plant is at least 20 d old). Emergence score was determined for each plot as follows: 100 x $\sum$ (number of plants emerged at time i/time from planting)/time from planting to end of emergence (Smith and Miller, 1964). The proportion of emergence (%) was also recorded for each plot. Under optimal temperature we measure days to emergence and proportion of emergence (%).

Data analyses. Data were analyzed with the GLM procedure of the SAS (2000) statistical package. The least significant difference (LSD) method ($P \leq 0.05$) was used to analyze differences between cultivar means for the quantitative traits evaluated. Standard errors and coefficients of variation were also calculated. Pearson correlation coefficients were computed for all traits measured (Steel et al., 1997).

Results and Discussion

Significant differences among the runner bean cultivars were noted for all agronomic characters evaluated, except for emergence score, indicating the existence of variation in the studied germplasm. The variation found is in agreement with Santalla et al. (2004) who reported differences for agronomic performance and seed quality among runner bean cultivars from Spain and Portugal. Scully and Waines (1987) also found significant differences among cultivars for germination under cold conditions in common and tepary bean. Alvarez et al. (1998) concluded that the runner bean cultivars maintained a high level of diversity after their introduction in the Iberian Peninsula. This process probably implied great changes in the structure of the genetic variation in the cultivars and a quick adaptation to the new conditions in different growing areas. The runner bean is a cross-pollinated species with medium to high variation within populations (Zeven et al. 1993). The outcrossing should explain the great amount of variation that exists in the various characters evaluated.

Table 2 displays the correlation between traits that showed significant differences among cultivars. Seed weight was also included in this analysis. Days to emergence was significantly and positively correlated with days to first trifoliate leaf (0.75**) and negatively with plant height at 20 d (-0.46*), and did not have significant correlation with seed weight. Rapid germination and emergence under stressful cold conditions would result in an early development of the plants, as shown by a faster expansion of the first trifoliate leaf and higher plants when compared with plants that emerged later. It is important to have germplasm that is able to grow quickly at early stages to grow runner bean under the stressful cold conditions of the early spring resulting in a good crop canopy later on during the growing season. Plant height at 10

and 20 d was positively correlated with shoot dry weight (0.68** and 0.75**). Seed weight was positively correlated with the shoot dry weight (0.42**). It is the only indicator of the influence of seed size in the development of plants under cold conditions. Therefore, the use of large-seeded cultivars of the runner bean could be regarded as an agronomic strategy under cold conditions for early sowing.

Table 3 shows the mean values and range of variation of the agronomic traits evaluated. The proportion of emergence at optimal temperature had an average value of 92.2% and a minimum value of 80.0% while at sub-optimal temperature it had an average value of 78.6% and a minimum value of 50.0%, indicating that in general all the cultivars were able to germinate under cold conditions. The proportion of emergence was generally acceptable under the two temperatures but at sub-optimal temperature (t1) it was lower than at optimal temperature (t2). Seven accessions (PHA-0011, PHA-0133, PHA-0311, PHA-0469, PHA-0664, PHA-1025, and Scarlet Emperor) presented a germination proportion >90% at sub-optimal temperature, similar to the score under optimal temperature. These results indicate that the proportion of emergence of seeds increases with temperature up to optimal conditions. The emergence was delayed at sub-optimal temperature (29 days) compared to the days to emergence under optimal temperature (7 days). In the field, the seeds were not able to germinate after 20 or more days inside to in the soil due to damping-off disease, incited by seed- and soil-borne fungi, such as *Rhizoctonia, Aphanomyces, Pythium, Phytophthora, Botrytis, Fusarium, Cylindrocladium, Diplodia, Phoma,* and *Alternaria*. The emergence of all cultivars under sub-optimal conditions (23–35 days) was greatly delayed compared with the standard field values for the north of Spain and Portugal (8-12 d). Scully and Waines (1987) found that germination of the common bean ranged from 16.3 to 23.8 d to

emergence at 12ºC. One reason for the superior performance of the runner bean cultivars could be due to the large seeds that may allow rapid imbibition of water during germination.

The earliness of the cultivars under cold conditions could be further assessed by combining the effect on emergence and the expansion of the first trifoliate leaf. Best performers were the cultivars PHA-0011 (26.3 d to emergence and 39.5 d to the expansion of the first trifoliate leaf), PHA-0163 (25.2 d and 40.2 d), PHA-1018 (23.7 d and 31.2 d), and PHA-1025 (22.6 d and 37.8 d). All lines/cultivars are large (>133 g 100 seed^{-1}) and white seeded. PHA-0011, PHA-1018 and PHA-1025 came from cool areas of central Spain and PHA-0163 from the temperate northwest. The cultivar NI-15c, a medium seeded (111.3 g 100 seed^{-1}) colored type from Rwanda also exhibited good performance (23.0 d and 42.0 d) while the cultivar from the highlands of Mexico, PI325592, with small (84.3 g 100 seed^{-1}) colored seeds had poor scores (35.4 d and 53.9 d). Two commercial cultivars, Painted Lady Bi-color (25.6 d and 42.6 d), with large colored seeds (142.0 g 100 seed^{-1}) and The Czar (26.9 d and 42.6 d), with medium (117.7 g 100 seed^{-1}) white seeds also exhibited moderate earliness.

The plant height at 10 and 20 d after emergence indicated the ability to grow under cold conditions. The best performers were Rwandan cultivars, NI-15c (138.6 mm at 10 d and 333.5 mm at 20 d) and NI-16c (147.0 mm and 297.8 mm). Four cultivars originally from temperate areas of the North of Spain had good post-emergence stem elongation: PHA-0133 (154.9 mm and 265.6 mm), PHA-0311 (148.3 mm and 277.0 mm), PHA-0409 (137.3 mm and 246.8 mm) and PHA-0664 (116.6 mm and 258.7 mm). The commercial cultivars had, in general, great ability to grow in low temperature as

displayed by Painted Lady Bi-color (141.7 mm and 297.2 mm), Scarlet Emperor (140.7 mm and 266.5 mm), and Carter's Streamline (134.3 mm and 261.7 mm).

The shoot and root dry weight after plants has grown at least 20 d under low temperatures are parameters for the estimation of vigor. The most vigorous were the commercial cultivars Scarlet Emperor (0.51 g shoot dry weight and 0.65 g root dry weight) and Painted Lady Bi-colored (0.58 g and 0.54 g) and the small white-seeded (85.0 g 100 seed^{-1}) Mexican cultivar PI510637 (0.49 g and 0.64 g). Some Spanish cultivars worth nothing for their good performance: PHA-1018 (0.54 g and 0.57 g), originated in a cool area, with white large (138.7 g 100 seed^{-1}) seeds, and four cultivars from temperate areas of the Northern Spain: PHA-0166c (0.47 g and 0.64 g), with medium (102.3 g 100 seed^{-1}) colored seeds, PHA-0311 (0.60 g and 0.44 g), PHA-0409 (0.47 g and 0.57 g), and PHA-0469 (0.47 g and 0.61 g), with white large (186.0 g 100 seed^{-1}) seeds.

Overall the results indicated that seven cultivars performed the best under the experimental cold conditions in the growth chamber: the commercial cultivars Painted Lady Bi-color and Scarlet Emperor, the Rwanda cultivar NI-15c and four white-seeded cultivars from the Iberian Peninsula: PHA-0011, PHA-0133, PHA-0311, PHA-0664, and PHA-1025. The relationship between superior commercial quality and high seed yield in runner bean germplasm is noteworthy. Santalla et al. (2004) reported the high culinary quality of PHA-0311 and PHA-1025, and the high yield of PHA-0311. These cultivars merit special attention for commercial use and for genetic material for breeding purposes. There may be a potential market for large white seeded runner bean cultivars as a substitute for white kidney beans. The range of new cultivars for food consumption could be increased and diversified.

Runner bean is considered a warm weather crop. It is generally accepted that runner bean was domesticated in warm areas from where it was moved to cooler regions. In some areas with cool and humid springs, such the European Atlantic coast, it would be useful to have cold-tolerant types that could be planted early to promote early pollination and harvest, avoiding summer drought and pests, and extend the growing cycle, to produce higher yields. Scully and Waines (1987) suggested that differences in the establishment of seedlings under cool conditions among common and tepary bean genotypes could be extrapolated to the field. The adaptation of runner bean to early planting requires a high percentage of emergence and vigorous seedling growth under cool temperatures. European runner bean, particularly the Spanish germplasm, came primarily from Mexico, Guatemala and Honduras and has been adapted to temperate conditions during the last four centuries. Furthermore, runner bean cultivars originating from the Atlantic European coast have some cold tolerance during early development and the ability to withstand the cool and wet springs. Other authors (Revilla et al., 2000) suggest that the ability to germinate and survive under cold conditions may be necessary, but these characteristics, by themselves, do not ensure early vigor. The germplasm studied represents a valuable source of genetic diversity that could potentially be highly useful for future breeding programs for runner bean. Selection within this germplasm could offer possibilities for the long-term generation of useful material. Furthermore, the runner bean cultivars that showed great ability to emerge and grow under cool conditions could be used as a source of cold tolerance in interspecific hybridization with common bean.

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1 *Table 1*. Origin, type of germination, seed color and seed weight of the runner bean accessions

2 evaluated under cold conditions

Accession [a]	Origin	Type of germination	Seed color	Seed weight (g 100 seed^{-1})
PHA-0011	Spain (Madrid)	hypogeal	white	167.3
PHA-0127	Spain (Galicia)	hypogeal	white	78.3
PHA-0133	Spain (Galicia)	hypogeal	white	90.7
PHA-0163	Spain (Galicia)	hypogeal	white	150.0
PHA-0166w	Spain (Galicia)	hypogeal	white	96.7
PHA-0166c	Spain (Galicia)	hypogeal	violet, speckled	102.3
PHA-0311	Spain (Galicia)	hypogeal	white	155.0
PHA-0322	Spain (Galicia)	hypogeal	white	151.3
PHA-0352	Spain (Galicia)	hypogeal	white	114.7
PHA-0409	Spain (Asturias)	hypogeal	white	116.3
PHA-0469	Spain (Galicia)	hypogeal	white	186.0
PHA-0605	Spain (Castilla y León)	hypogeal	white	84.0
PHA-0664	Portugal (Tras-os-Montes e Alto Douro)	hypogeal	white	154.0
PHA-1018	Spain (Navarra)	hypogeal	white	138.7
PHA-1023w	Spain (Castilla y León)	hypogeal	white	180.7
PHA-1023c	Spain (Castilla y León)	hypogeal	violet, speckled	135.3
PHA-1025	Spain (Castilla y León)	hypogeal	white	133.0
PHA-1031	Spain (Castilla y León)	hypogeal	white	285.3
PHA-1029	Spain (Castilla y León)	hypogeal	white	116.3
PI325592	Mexico	hypogeal	violet,brown,speckled	84.3
PI510637	Mexico	hypogeal	white	85.0
PI313313	Mexico	epigeal	light brown	38.0
PI325608	Mexico	epigeal	violet,brown,speckled	46.0
PI535276	Mexico (wild population)	epigeal	brown	9.0
NI-15w	Rwanda	hypogeal	white	107.0
NI-15c	Rwanda	hypogeal	violet, speckled	114.0
NI-16w	Rwanda	hypogeal	white	116.0
NI-16c	Rwanda	intermediate	violet, speckled	93.7
Sutton's Prizewinner	Commercial (Thomas Etty Esq)	hypogeal	violet, speckled	104.7
The Czar	Commercial (Thomas Etty Esq)	hypogeal	white	117.7
Painted Lady Bi-color	Commercial (Thomas Etty Esq)	hypogeal	violet, speckled	142.0
Carter's Streamline	Commercial (Thomas Etty Esq)	hypogeal	violet, speckled	105.7
Scarlet Emperor	Commercial (Thomas Etty Esq)	hypogeal	violet, speckled	111.3

3 [a] w=white, c=colored

Table 2. Correlations coefficients between agronomic traits in the runner bean cultivars evaluated under cold conditions.

	Emergence (%)		Time to emergence (days)		First trifoliate leaf (days)		Plant height 10 d (mm)		Plant height 20 d (mm)		Shoot dry weight (g)		Root dry weight (g)		Seed weight (g)
Proportion emergence (%)	1.00														
Emergence (days)	-0.64	**	1.00												
First trifoliate leaf (days)	-0.29	NS	0.75	**	1.00										
Plant height 10 d (mm)	0.66	**	-0.33	NS	-0.13	NS	1.00								
Plant height 20 d (mm)	0.68	**	-0.46	*	-0.31	NS	0.92	**	1.00						
Shoot dry weight (g)	0.46	*	-0.26	NS	-0.28	NS	0.68	**	0.75	**	1.00				
Root dry weight (g)	0.14	NS	0.10	NS	0.09	NS	0.27	NS	0.20	NS	0.50	**	1.00		
Seed weight (g)	0.15	NS	-0.24	NS	-0.32	NS	0.18	NS	0.32	NS	0.42	**	0.03	NS	1.00

NS, *, **Nonsignificant or significant at $P \leq 0.05$ or 0.01, respectively

Table 3. Mean, minimum and maximum for emergence at two temperature conditions and agronomic traits of runner bean cultivars evaluated under sub-optimal temperature.

Accessions	Emergence (%)		Days to emergence		Days to first trifoliate leaf	Emergence score	Plant height 10 d (mm)	Plant height 20 d (mm)	Shoot dry weight (g)	Root dry weight (g)
	t1[a]	t2[a]	t1	t2[z]						
PHA-0011	96.7	100.0	26.3	6.7	39.5	5.7	126.8	242.7	0.56	0.32
PHA-0127	53.3	80.0	33.0	10.0	48.4	3.1	67.0	111.6	0.28	0.25
PHA-0133	100.0	93.3	25.0	6.7	43.7	5.8	154.9	265.6	0.37	0.40
PHA-0163	86.7	100.0	25.2	6.7	40.2	4.9	106.2	223.9	0.41	0.43
PHA-0166c	86.7	80.0	28.5	7.0	48.8	5.6	117.3	202.0	0.47	0.64
PHA-0166w	56.7	80.0	28.6	6.7	50.9	3.7	79.3	137.3	0.33	0.32
PHA-0311	93.3	93.3	24.9	6.7	47.9	5.4	148.3	277.0	0.60	0.44
PHA-0322	73.3	100.0	27.9	6.7	46.8	4.6	88.2	168.3	0.48	0.43
PHA-0352	83.3	100.0	25.7	6.7	41.6	4.9	90.0	164.3	0.27	0.22
PHA-0409	73.3	93.3	29.9	6.7	48.3	4.6	137.3	246.8	0.47	0.57
PHA-0469	90.0	100.0	27.0	6.7	43.9	5.5	110.6	238.2	0.47	0.61
PHA-0605	63.3	86.7	28.7	6.7	48.8	4.2	79.3	152.8	0.26	0.27
PHA-0664	96.7	100.0	27.0	6.7	41.6	6.1	116.6	258.7	0.43	0.21
PHA-1018	76.7	93.3	23.7	6.7	31.2	4.2	95.4	199.9	0.54	0.57
PHA-1023c	86.7	100.0	26.6	6.7	45.0	5.3	115.4	217.6	0.45	0.21
PHA-1023w	83.3	100.0	26.0	6.7	42.8	5.0	104.1	201.3	0.43	0.25
PHA-1025	96.7	100.0	22.6	6.7	37.8	5.1	117.3	210.9	0.38	0.28
PHA-1031	70.0	93.3	28.6	8.3	45.3	4.7	111.9	243.3	0.53	0.45
PHA-1029	83.3	100.0	27.0	6.7	44.7	5.3	103.6	194.1	0.45	0.41
PI325592	50.0	83.5	35.4	7.0	53.9	4.1	81.3	125.2	0.35	0.44
PI510637	70.0	100.0	32.5	7.0	48.0	5.1	99.8	160.6	0.49	0.64

Table 3. Continued

Accessions	Emergence (%)		Days to emergence		Days to first trifoliate leaf	Emergence score	Plant height 10 d (mm)	Plant height 20 d (mm)	Shoot dry weight (g)	Root dry weight (g)
	t1[a]	t2[a]	t1	t2[z]						
NI-15c	80.0	100.0	23.0	6.7	42.0	4.3	138.6	333.5	0.58	0.41
NI-15w	66.7	100.0	25.6	6.7	43.4	3.9	113.7	244.7	0.51	0.37
NI-16c	70.0	100.0	29.6	6.7	44.1	4.8	147.0	297.8	0.60	0.44
NI-16w	70.0	100.0	26.2	6.7	46.4	4.3	68.6	142.8	0.32	0.34
Sutton's Prizewinner	86.7	100.0	29.6	8.3	51.1	6.0	114.9	232.7	0.43	0.35
The Czar	83.3	100.0	26.9	6.7	42.6	5.1	121.4	231.3	0.44	0.30
Painted Lady Bi-color	86.7	100.0	25.6	6.7	42.6	5.0	141.7	297.2	0.58	0.54
Carter's Streamline	76.7	80.0	27.4	8.3	46.6	4.9	134.3	261.7	0.45	0.26
Scarlet Emperor	100	93.3	26.6	6.7	48.6	4.6	140.7	266.5	0.51	0.65
Mean	78.6	92.2	28.8	7.4	44.9	4.9	112.4	218.3	0.45	0.40
Minimum	50.0	80.0	22.6	6.7	31.2	3.1	67.0	111.6	0.26	0.21
Maximum	100.0	100.0	35.4	10.0	53.9	6.1	154.9	333.5	0.60	0.65
LSD[b]	21.5	14.0	2.37	4.4	3.68	1.7	24.36	41.81	0.11	0.23

[a] t1,sub-optimal temperature, t2, optimal temperature

[b] Least significant difference at $P \leq 0.05$